FURTHER OBSERVATIONS OF THE FEEDING ECOLOGY
OF POSTLARVAL PINFISH, *LAGODON RHOMBOIDES*,
AND SPOT, *LEIOSTOMUS XANTHURUS*[1]

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ABSTRACT

The effect of current on feeding, temporal variation in food consumption, and the effect of predator and prey size on food preferences were evaluated for postlarval stages of pinfish, *Lagodon rhomboides* (15-19 mm total length); and spot, *Leiostomus xanthurus* (16-22 mm). Field and laboratory observations indicated that pinfish feeding rates decreased as water current velocity increased. Similar behavior was noted in spot from field observations, but spot feeding rates in the laboratory were highest when a slight current was present. Mean gut contents of postlarvae collected at midday over a 2-mo period ranged from 0.4 to 38 copepods/fish. The mean coefficient of variation for the number of copepods per fish in a single midday sample (*n* = 20 fish) was 20%. Maximum daily feeding rates were estimated at 17 and 26 copepods/h for spot and pinfish, respectively. Field and laboratory data confirmed that as postlarval size increases the size of their prey also increases. Refined estimates of postlarval evacuation rates and daily rations also are presented. Daily ration estimates as a percent of the fish's wet body weight were 9% for both species. The ration estimates for both species were greater than metabolic needs estimated from oxygen consumption measurements.

Information on the feeding ecology of larval fishes is necessary to understand the role of larvae in ecosystem energetics and community structure and the importance of feeding conditions to year class strength. However, relatively little is known about the feeding of larval fishes. This paper reports four major aspects of postlarval feeding: 1) the effect of current speed on feeding intensity; 2) temporal variation in postlarval food consumption; 3) the relation of feeding rate to food abundance; and 4) the effect of prey and predator size on postlarval food preferences. Refined results concerning postlarval evacuation rates and daily rations also are presented. Our earlier paper (Kjelson et al. 1975) stressed the study of food preferences, feeding intensity and periodicity, evacuation rates, daily rations, and the effect of handling and capturing the fishes on their digestive tract contents.

Pinfish, *Lagodon rhomboides*, and spot, *Leiostomus xanthurus*, constitute a major portion of the fish biomass of southeastern estuaries of the Atlantic coast and thus are important to the structure and function of these ecosystems. Spot are also an important commercial food species.

Both species are primarily winter spawners in the Atlantic Ocean with larvae migrating inshore to estuarine waters which serve as nursery grounds between spring and fall. Larval forms (here defined as individuals <11 mm) are rarely found within the estuaries, whereas postlarval stages (here defined as fish between 11 and 22 mm) occur both in nearshore oceanic and estuarine waters.

METHODS

General

Postlarval pinfish (15-19 mm total length (TL)) and spot (16-22 mm) were collected during January and February 1974, from the Newport River estuary, N.C., following their recent immigration into the estuary from the offshore spawning grounds in the Atlantic Ocean. All fish were collected at Pivers Island, 2.5 km inside the Beaufort Inlet. Shore samples were collected with dip nets while those in the adjacent channel were collected with a channel net (Lewis et al. 1970). Fish were anesthetized immediately upon capture in a 0.12 g/liter seawater solution of MS-222[3] (tricaine methanesulfonate) and dissected in the

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

laboratory. Gut contents included material in the total digestive tract, from foregut to anus.

Current Speed and Feeding Intensity

Larval pinfish and spot were collected within 2 m of the shore (depth 0-2 m) where refuge from current was available and in the center of the adjacent channel (depth 5-7 m) approximately 25 m from shore where a current normally was present. Three separate collections were made for pinfish and two for spot. Twenty fish of each species from each collection were measured, dissected, and the mean number of copepods per fish determined. Surface tows for zooplankton were made at the same time and location using a 30 cm in diameter, 0.158-mm mesh net with current meter attached. Observations on copepods throughout this investigation were restricted to adult and copepodid stages. Copepod measurements were made of carapace length. Current velocities were measured with a Gurley current meter.

Feeding rates of pinfish and spot at varied current speeds also were studied in the laboratory. Fish were captured, placed in four donut-shaped, 11-liter tanks (46 cm in diameter, 10- by 10-cm cross-sectional area), and allowed to acclimate overnight in filtered, food-free seawater with no current flow. Two tanks were used as controls (zero current flow) and contained 50 and 100 fish, respectively. The other two tanks, containing 50 fish each, were attached to pumps, providing current velocities of 1.7 and 5.1 m/s, respectively. Current speed was estimated by recording the amount of time required for a minute innate particle to complete one revolution of the donut-shaped tank. At the beginning of each experiment, current flow was started in the two test chambers and *Artemia salina* nauplii (1.0/ml) were provided to each of the four tanks. Fish were allowed to feed for 1 h with additional food provided after 30 min to assume a minimum density of 1 *Artemia*/ml throughout the experiment. Twenty fish were sampled from each tank to calculate the mean number of *Artemia* consumed.

Temporal Variation in Midday Feeding

Day-to-day variation in the feeding intensity of larval pinfish and spot was studied at midday (1100-1300 h) when larval digestive tracts con-

tained the greatest amounts of food. Fifteen collections were made from 21 January to 28 February at one site within 2 m of the shore. Each collection consisted of 20 fish of each species. Total lengths of the fish were measured, the total number of copepods in each gut counted, and a geometric mean of the number of copepods per fish calculated. Geometric means were used as a measure of central tendency because frequency distributions of the copepods or *Artemia* nauplii per fish showed a positive skewness. In addition, a geometric mean was used to limit the bias of a few individuals feeding at a rate not representative of the population because variation increased as the mean values increased.

A zooplankton tow was taken at the time and location of fish capture. The tows were made just below the surface, against the current, and sampled approximately 5 m³ of water. Estimates of copepod density were made from three 10-ml subsamples of each tow. Twenty copepods per sample were measured for length frequencies.

Evacuation Rates

To refine our information on larval evacuation rates of copepods, two laboratory experiments were performed using pinfish and spot that had been fed an abundance of natural copepods. Four to five hundred fish were starved for 8 to 12 h and then they were allowed to feed for 1 h. Food densities averaged 2.5 copepods/ml for pinfish and 3.0 copepods/ml for spot. Larvae were acclimated and experiments run at ambient estuarine temperatures and salinities. Temperature was 12°C for the pinfish evacuation and 17°C for spot; salinity was 30‰. Following feeding, 30 fish were removed, anesthetized with MS-222 to prevent any possible regurgitation, dissected, and counts made of the numbers of copepods per fish. At the same time, three groups of 100 fish were transferred to separate food-free tanks, and the decrease in their gut contents observed by sampling 10 fish from each tank at 2-h intervals until more than one-half of the fish had empty tracts. Instantaneous evacuation rates were then calculated according to the method of Peters and Kjelson (1975). The amount of food remaining in the stomach at any time can be predicted from the following equation:

$$\log C = \log A + Bt$$

where C = content of gastrointestinal tract + 1

A = amount ingested + 1
B = evacuation rate constant
t = time.

By adding 1 to the amount ingested and to gut contents we were able to include empty gastrointestinal tracts in our calculations. From the above equation, with log base 10:

$$C = e^{2.303\,(\log A\, +\, Bt)}$$

and the instantaneous evacuation rate

$$\frac{dC}{dt} = 2.303\,Be^{2.303\,(\log A\, +\, Bt)}$$

or

$$\frac{dC}{dt} = 2.303\,BC.$$

Feeding Periodicity

Diel periodicity of digestive tract contents indicated the intensity and chronology of feeding by the fish. Our purpose was to refine the feeding chronology curve (Kjelson et al. 1975) by taking samples more frequently than in our previous study. Ten fish of each species were collected at 2-h intervals between 0600 and 1800 and at 2100 and 2400 h. Fewer samples were taken at night because our past observations have shown that larval fish cease feeding during darkness. All fish were measured, the copepods they contained counted, and a geometric mean for copepods per fish calculated for each sample.

Daily Rations

One objective of this research was to re-estimate the daily ration of larval fish for comparison with our earlier study. Daily rations were calculated by the same technique (Kjelson et al. 1975) using new information on diel periodicity of gut contents and refined measurements of instantaneous evacuation rates. Our method of calculating daily ration accounts for changes in evacuation rate which accompany diel changes in feeding intensity.

To calculate daily ration, we first estimated the average evacuation rates (in copepods per hour) for each of the 2-, 3-, or 6-h sampling periods in our feeding chronology study. This average rate was the geometric mean of the instantaneous evacua-

tion rates at the beginning and end of each period. The estimate of food evacuated during any period is equal to the number of hours in the period multiplied by the respective average hourly evacuation rate. The total food evacuated per day was computed by summing the nine respective evacuation estimates, and is an estimate of the daily ration because the average ingestion rate must equal the rate at which material in the gut is assimilated or defecated.

Daily rations were calculated initially as copepods per fish per day and then transformed to percent of the larval body weight and calories per fish per day. Dry weights of ingested copepods were estimated from the length-weight relationship: $W = 6.274L - 0.153$ where W is the dry weight in micrograms and L is the copepod length in millimeters, based upon Heinle's (1966) data for all stages of Acartia tonsa. Copepod dry weights were converted to wet weights using a factor of 9.1 based upon our measurements of the wet-dry ratio for zooplankton and were compared with wet weights of the fish to compute the daily ration as a percent of live body weight. Daily caloric intake was computed using our estimation of 0.555 cal/mg wet weight of an average size copepod, based on micro-bomb calorimeter measurements of mixed estuarine zooplankton (Thayer et al. 1974).

RESULTS AND DISCUSSION

Effects of Current Speed on Feeding Intensity

Pinfish and spot larvae collected along the shore had more copepods present in their digestive tracts than those collected in midchannel (Table 1). Previous observations (Kjelson et al. 1975) indicated that neither pinfish nor spot regurgitate or defecate food under the stress of capture or handling. Thus, differences in collecting techniques

TABLE 1. — Digestive tract contents of larval fishes collected at midday at midchannel and shore stations in the Newport River estuary, January to February 1974.

Date	Species	Mean number of copepods/fish ± 1 SE		Current speed (m/s) in channel[1]	Tidal stage[2]
		Shore	Channel		
29 Jan.	Pinfish	9.1 ± 1.6	0.8 ± 0.2	1.4	LF
30 Jan.	Pinfish	19.6 ± 2.8	4.1 ± 0.8	0.0	HS
14 Feb.	Pinfish	20.0 ± 2.8	1.8 ± 0.6	3.2	LF
14 Feb.	Spot	14.4 ± 1.7	0.9 ± 0.4	3.2	LF
21 Feb.	Spot	2.7 ± 0.6	0.3 ± 0.2	5.5	ME

[1]No current was observed along the shore on any sample date.
[2]LF = late flood, ME = mid ebb, HS = high slack.

(channel net versus dip net) between areas were not felt to bias the results. We observed no differences in the length of fish sampled (by species) or in the density of copepods at the two locations.

These results indicate that larval feeding rates are limited when the fish are exposed to current. Current speed ranged from 0 to 5.5 m/s in mid-channel where feeding was low, to no measurable current along the shore where more feeding occurred (Table 1). In addition, pinfish collected in the channel on a slack tide contained 4.1 copepods/fish compared with a mean of 1.3 copepods/fish when there was a current present.

Laboratory experiments indicated that current speed affected the food consumption rate of both species (Table 2). Pinfish consumed the most food when there was no current, but spot ate more at a current velocity of 1.7 m/s. Pinfish ate the least food in a 5.1 m/s current while the spot minimum feeding occurred at varied current speeds. Both species fed at a higher rate when fish densities were lower.

The observations from both field and laboratory studies indicate that postlarval pinfish feeding declines as current speed increases. These results suggest that current speed influences the ability of pinfish to capture their prey, although the specific reasons for such altered behavior are unknown. The well-known attack behavior of larval fish, that of visually sighting the prey and of assuming an S-shape prior to striking (Blaxter and Holliday 1963), may be unattainable by postlarval pinfish exposed to higher current speeds. Bishai (1959) found that larval herring drift with a current at speeds less than the current itself. This may suggest that the size, shape, and behavior of a plankter may influence its rate of movement in a current. Prey organisms may move at a faster rate than the fish larvae, which in turn may lessen the ability of the fish to orient to the prey.

Current also may destroy the microstructure of the prey population. Without a strong current, food could aggregate in patches thus producing local areas with high food density and therefore increase the rate of ingestion. This latter explanation is probable in the natural environment; however, it appears unlikely under the laboratory conditions, because the density of Artemia in the tanks was very high (1/ml) and prey were replenished to assure that it did not decrease. In addition, the small cross-sectional area (100 cm²) and volume of the tanks greatly limited the distance a larva had to travel to find food even if prey were in a patch configuration.

Differences in channel versus shoreline feeding by spot in the natural environment (Table 1) are similar to those of pinfish; however, feeding by spot in the laboratory was highly variable and is difficult to explain. Spot fed at the highest rates when a slight current was present and even fed at a high rate when exposed to a maximum current of 5.1 m/s. The spot postlarvae used in the studies were larger than the pinfish and this may explain the ability of spot to feed at a high rate when exposed to current, because increased size usually improves swimming ability which may improve the fish's ability to capture their prey. However, species differences in swimming ability were not apparent: larvae of both species moved freely about the tank when current was absent; oriented into the current or at times drifted with the current at the 1.7 m/s speed; and drifted along with the current in the 5.1 m/s current, although some individuals oriented into the current briefly. Similar behavior by larval fishes exposed to varied current velocities was discussed by Bishai (1959) and Houde (1969). Ryland (1963) indicated that the mechanisms by which larval fishes orient to a current are poorly understood. The lower feeding rate of spot in no current is unexplainable unless this species is adapted in some way to be more effective at capturing prey within a current. Serebrov (1973) also found differences in the feeding intensity of various species (guppy, *Poecilia reticulata,* and European dace, *Phoxinus phoxinus)* when exposed to different current velocities and suggested that the differences were due both to natural adaptation to certain current condi-

TABLE 2.—Digestive tract contents (mean number of *Artemia* nauplii/larva ± 1 SE) of larval fishes following feeding in the laboratory under several current velocities.

Date 1974	Species	Length of fish (mm)	Current velocity			
			[1]5.1 m/s	[1]1.7 m/s	No current[1]	No current[2]
26 Feb.	Pinfish	16-17	2.5 ± 1.8	22.1 ± 3.5	50.9 ± 6.3	35.0 ± 4.0
3 Mar.	Spot	20-22	104.7 ± 7.5	166.0 ± 8.0	72.1 ± 7.7	23.5 ± 5.3
14 Mar.	Spot	19-20	30.3 ± 3.3	90.0 ± 5.5	39.1 ± 4.3	23.1 ± 3.2

[1]Fifty fish.
[2]One hundred fish.

tions and to the stimulation of food grasping activity caused by the increased movement of food in a current.

The highly variable nature of spot feeding in the laboratory also may be explained by the varied current conditions within the tank itself, although conditions were kept as constant as possible during the two studies. Current flow may not have been uniform throughout the tank, although the importance of this factor upon feeding is unknown. The larvae in all experiments were distributed throughout the tank and did not appear to be feeding at specific locations. The low variability in feeding rate between individual fish in each experiment, as shown by the standard errors (Table 2), suggests that all individuals were feeding at a similar rate even though they were dispersed throughout the tank. The distribution of flow across the tank vertically was not measured, although such information would be useful (Ryland 1963). The two treatment groups of spot postlarvae were from separate field collections which may have altered their behavioral characteristics sufficiently to produce the variable results.

Finally, the apparent necessity for low current velocity for feeding to take place may restrict considerably the amount of area suitable for feeding to be successful. This may be particularly true along the channels linking the oceanic habitat to that of the estuarine marsh system where our observations took place. The amount of protected shoreline and bottom habitat characterized by low current velocity along these channels is very limited compared to that present in the broad reaches of the estuary where cordgrass (*Spartina*) marsh shoreline and eelgrass (*Zostera*) beds are extensive.

Temporal Variation in Food Consumption

Considerable day-to-day variation was observed in the mean number of copepods in the plankton and in the larval fish collected at midday (Figure 1). Mean pinfish gut contents ranged from 0.4 to 38 copepods/fish while spot contained from 0.5 to 24 copepods/fish. The coefficient of variation for the number of copepods per fish in single field samples averaged 20% (range 7-40%) for pinfish, and 17% (range 8-40%) for spot. The greatest variability occurred when the average gut contents were low. Copepod density also fluctuated widely from 477 to 3,262 copepods/m^3. These densities are not dis-
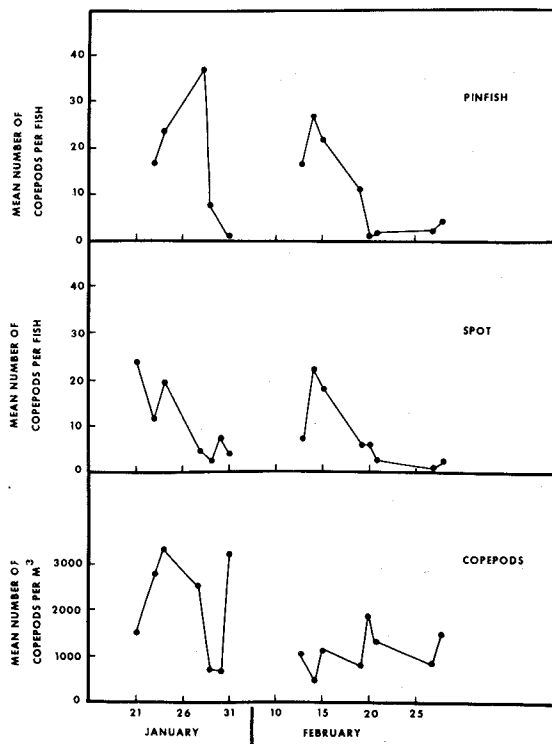

FIGURE 1. — Variation in the numbers of copepods per larval pinfish and spot, and copepods per cubic meter based on midday samples in the Newport River estuary during January and February 1974.

similar from those observed during the same months in the open waters of the Newport River estuary (Thayer et al. 1974). The coefficient of variation of the copepod counts from five tows at the site of larval collections was 24%. Such variation is not high for field sampling and although it represents the variability for only a single sampling date, it does suggest that the precision of the estimate of copepod density is acceptable.

One of our goals was to determine if the amount of food present in larvae was related to copepod density. In our study, the correlation coefficients between copepod concentration and gut contents were very low ($r = +0.08$ for both pinfish and spot), indicating that there was no relationship. Other studies on larval fish populations have shown that feeding incidence may be correlated with food concentration (Berner 1959; Nakai et al. 1966; Bainbridge and Forsyth 1971), while Houde (1967) found no correlation between copepod abundance and feeding rate by larval walleye.

The number of factors influencing larval feeding

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rates in an estuary are undoubtedly numerous; therefore, it may be difficult through field measurements to establish a relationship between larval feeding rates and food abundance. For example, the clumped distribution typical of zooplankton populations may affect larval feeding rates, with feeding limited primarily to those periods when the fish are exposed to a dense patch of copepods.

Comparing naturally occurring mean food densities with mean gut contents, to establish a relationship between prey abundance and feeding rate, presents problems if the zooplankton populations are not randomly distributed or if the fish collected were not feeding upon the same prey community sampled by the plankton net (O'Brien and Vinyard 1974). Furthermore, the aggregation of zooplankton discussed earlier may be important in determining the rate of food consumption (Schumann 1965). Ivlev (1961) indicates that patchiness in the distribution of the food material increases the ration by comparison with an even food distribution when the average concentration is the same in both cases. High consumption rates by postlarval pinfish and spot may be possible only when patches of copepods come within the feeding range of the larvae. This hypothesis is discussed by Murphy (1961). The above remarks emphasize that laboratory investigations may be required in understanding the relationships between feeding rates and food abundance.

Size Related Food Preferences

Various investigators have observed selective feeding by larval fish and, at times, definite preference for a specific food form is indicated. Much of the selectivity, however, is due to the size relationship of the larval fish and the available zooplankton (Marak 1960). Information gained from our midday field samples and our laboratory evacuation experiments enabled us to observe the relationship between fish size and the size of prey they consumed. The Wilcoxon test for paired values (Alder and Roessler 1964) was used to determine if the mean size of copepods consumed was significantly different (α = 0.05) from those collected in the plankton tows or provided in aquaria.

The spot collected for both field and laboratory studies were significantly larger than the pinfish. Both field and laboratory results indicated that pinfish larvae always ate smaller copepods than

the mean size available to them while the reverse was true for spot (Table 3). Each species consumed prey that were proportional to their size with the ratio of the mean copepod length to the average fish length approximately 1:35 based upon laboratory measurements to 1:30 based upon field data.

The above results suggest that, as the larval fish size increases, the size of the consumed prey also increases. Many researchers (Blaxter and Holliday 1963; Blaxter 1965; Ciechomski 1967; Detwyler and Houde 1970; de Mendiola 1974; Marak 1974) also have observed this relationship in a variety of larval fishes. However, the mean size consumed in each study by either pinfish or spot varied considerably (Table 3). Pinfish of similar mean sizes (16 and 16.4 mm) fed upon 590-μm copepods in the laboratory, but the 460-μm prey in the field. This difference in prey size may be explained by the apparent difference in the prey sizes available to the fish in the two studies; laboratory prey had a mean size of 663 μm while those in the field were only 515 μm. Spot size preferences, on the other hand, are difficult to explain in the same manner, because spot consumed larger prey in the laboratory than in the field, although the prey available in the laboratory were considerably smaller than those present in natural waters (Table 3).

TABLE 3.— Mean sizes of copepods eaten by larval pinfish and spot in the field and laboratory compared to the mean sizes of copepods present.

| Species | Larvae (mm) | Mean length of | |
		Copepods eaten (μm ± 1 SE)	Copepods in aquaria or net tow (μm ± 1 SE)
Laboratory:			
Pinfish	16.0	590 ± 29	663 ± 28
Spot	17.7	669 ± 31	491 ± 68
Field:			
Pinfish	16.4	460 ± 12	515 ± 22
Spot	20.4	581 ± 12	515 ± 22

Comparisons of mean size prey from plankton tows to those from gut contents may be difficult again due to distributional dissimilarities of both predator and prey populations during feeding and prey aggregation patterns (Schumann 1965; O'Brien and Vinyard 1974). However, these problems were lessened in laboratory aquaria where we were able to control the size, density, and distribution of the predator-prey populations.

Two primary factors appear to explain the increase in prey size as larval fish size increases.

First, mouth size usually increases as the length of larvae increases. This relationship has been documented for larval fish of various species by Marak (1960), Blaxter (1965), Ciechomski (1967), Detwyler and Houde (1970), and Shiroto (1970). A few body measurements of pinfish and spot postlarvae showed that the gape of the mouth increased as the size of the fish increased. Pinfish of 16 mm TL were estimated to have a mouth gape of 1.43 mm, while spot of 1.6 mm had a gape of 1.70 mm. The larger gape in spot may explain, in part, their consumption of larger prey. Secondly, swimming speed also increases with an increase in the fish's body size (Houde 1969; Hoagman 1974); hence, the large spot may be capable of capturing larger copepods.

Although this study emphasized the food size preferences of postlarval pinfish and spot, a topic of potential importance in the selective nature of larval fish feeding deals with the selection of specific species of copepods. We did not compare the copepod taxa in the digestive tracts with those found in the plankton tows, but such effort should provide valuable information, because copepod species differences in swimming speed, vertical position in the water, and aggregation behavior may be very important in determining the type of prey available to and finally consumed by larval fish. However, the dominant genera present in the estuary during the study period were *Centropages, Temora, Acartia,* and *Euterpina,* common forms in the Beaufort area during winter and early spring (Thayer et al. 1974). Marak (1960) and Ciechomski (1967) attempted to assess the selectivity of larval fish for individual species of copepods, but did not observe any such preferences.

The size differences in spot and pinfish that we observed in the Newport River estuary may be due either to dissimilar spawning times, different growth rates, or both. Observations made in another North Carolina estuary (the White Oak River estuary) during 1969 indicated that estuarine spot and pinfish larval populations during January and February differed in size and that spot were significantly larger than pinfish (R. M. Lewis, pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.); spot average 18.0 mm in length while pinfish were 15.5 mm. Thus, there appears to be consistancy in the size differences observed in these two species during their influx into North Carolina estuarine waters.

Evacuation Rates

Regression coefficients for the equations describing the evacuation of copepods by larval pinfish and spot are shown in Table 4. The coefficients differ significantly from those calculated earlier (Kjelson et al. 1975). Copepod evacuation in our previous study was determined using fish collected in the estuary, placing them in a food-free environment, and observing evacuation. Those fish contained limited amounts of food at the beginning of the experiments apparently due to a low rate of feeding just prior to capture. Also, there was a 2°C difference between estuarine and laboratory water temperatures, and this may have altered the evacuation rates.

In an effort to measure the evacuation through a wide range of gut quantities and thus, hopefully, achieve a better description of evacuation, our present study used fish that initially had their guts full of copepods (21-57 copepods/fish) as determined from sacrificing 20 fish of each species at the beginning of the experiment. In addition, the possible stress of transport and rapid temperature changes in the earlier study were eliminated by using fish that had been acclimated to laboratory temperatures and that were fed in the laboratory.

The regression coefficients (slopes) achieved from our present study (Table 4) were significantly different from and approximately twice those found during the 1972-73 evacuation experiments. We consider the estimates of evacuation rates in the present study to be more representative of natural evacuation because the techniques used in measuring evacuation were more refined than in the earlier study.

The experimental temperatures, although different for the two species, were within the normal range for larvae immigrating into North Carolina estuaries. The larger negative slope in the regression model for spot compared with that for pinfish (Table 4) is probably due in part to the temperature differences (12°C for pinfish and

TABLE 4.—Linear regressions describing evacuation of copepods in pinfish and spot larvae. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of copepods per larva})$ and t = hours since feeding. n = number of data points.

Species	Size range (mm)	Temperature (°C)	A	B	n	r^2
Pinfish	15-18	12	1.30	-0.18	5	0.98*
Spot	16-20	17	1.84	-0.24	5	0.98*

*$P < 0.01$

17°C for spot), because Peters et al. (1974) showed that evacuation rate of juvenile pinfish and spot is related directly to temperature.

Feeding Periodicity and Feeding Rate

Observations of larval gut contents through 24 h again indicated that these larval fish contained the greatest amount of food during daylight hours (Figure 2). Peaks in gut contents for both pinfish and spot were at 1200 h. Water temperature was 15°C.

The periodicity observed in the gut contents does not represent the actual feeding periodicity. However, if our evacuation data and model are appropriate, the feeding periodicity may be calculated from the periodicity of gut contents. Gut contents at the beginning and end of each sampling interval (Figure 2) differ by an amount equal to the amount consumed minus the amount evacuated during that time period (Peters and Kjelson 1975). Thus, we can add the amount evacuated in each interval from the change in gut content to achieve the amount ingested during the interval. Maximum hourly feeding rates (from the 1000-1200-h sampling interval) were 26 copepods/h for pinfish and 17 copepods/h for spot.

Daily Rations

Estimates of daily ration for pinfish and spot larvae were higher than those obtained from the 1972-73 study. During our earlier study, pinfish ate 38 copepods/day while the present estimate indicates 92. Previous estimates for spot were 47 and 99 copepods/day while our present estimate is 115 (Table 5). The increased ration sizes are attributed to the use of higher instantaeous evacuation rates, and in the case of pinfish, to the presence of greater amounts of food during the feeding periodicity study (Figure 2). Pinfish di-
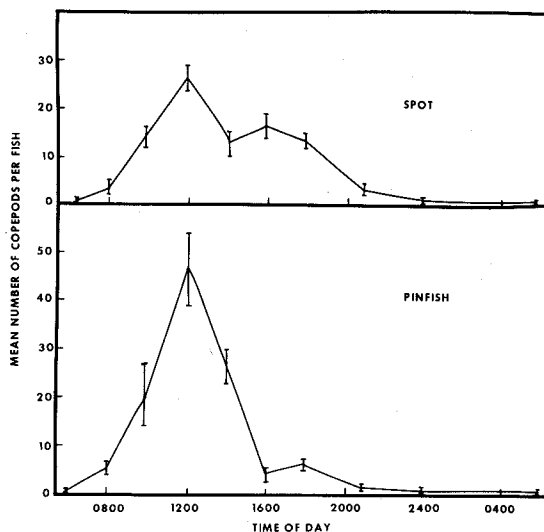

FIGURE 2. — Diel cycle of digestive tract contents in larval pinfish and spot at 15°C based upon the geometric mean of the number of copepods per fish ($n = 10$ fish per sampling time). Vertical bars are equal to two standard errors.

gestive tracts had an average of 47 copepods/fish at 1200 h during the 1974 sample day whereas during 1972 they only had 10 copepods/fish. Spot gut contents at 1200 h averaged 17, 37, and 27, respectively in the three successive years of the study.

Based on our daily ration estimates of 1.3 and 2.0 cal/fish per day (Table 5) and the mean weights of the larvae, this was equal to a consumption rate of approximately 0.05 cal/mg fish wet weight per day for both species. The similarity is interesting since the average pinfish weight was only 60% that of spot and suggests that larvae of dissimilar species and sizes have similar consumption on a unit weight basis. Oxygen consumption measurements by D. E. Hoss (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.) indicate that similar respiration

TABLE 5.—Daily rations calculated from feeding studies and O_2 consumption measurements at 15°C for larval pinfish and spot in the Newport River estuary, N.C.

Species	Mean larvae wet wt (mg)	Number copepods/ fish · day	Calories/ fish · day	Calories/fish · day from O_2 consumption[1]	
				Gilson respirometer[2]	Flowing water respirometer[3]
Pinfish	25	92	1.3	0.9	1.0
Spot	42	115	2.0	1.3	2.0

[1]3.38 cal/mg O_2.
[2]Pinfish data from Hoss (1974), spot data from D. E. Hoss (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.).
[3]Pinfish data from W. F. Hettler, Jr. (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.), spot data from Hoss et al. (1974).

values on a per unit weight basis are typical for larvae of different species. Such similarity, however, may not exist for all species and size classes.

Measurements of postlarval metabolic expenditures based on oxygen consumptions at 15°C using a Gilson respirometer (Hoss, pers. commun.) and a flowing water respirometer (W. F. Hetter, Jr., pers. commun., Atlantic Estuarine Fisheries Center) are shown in Table 5. In both cases, fish were deprived of food for 24 h prior to measurement of their oxygen consumption, and the oxygen content of the water was near air saturation. Both Hoss and Hettler consider their measurements to be routine oxygen consumption as defined by Fry (1971), i.e., the mean rate observed in fish whose metabolic rate is influenced by random activity under experimental conditions in which movements are presumably somewhat restricted and the fish are protected from outside stimuli. Postlarval pinfish and spot in the flowing water respirometer were confined in an 11-liter chamber identical to that used for our laboratory current-feeding experiments described earlier and therefore were able to move about considerably.

A major problem exists in most measurements of fish oxygen consumption due to the uncertainty as to the animals state of activity (Altman and Dittmer 1971). Furthermore, measurements of fish respiration under natural conditions, termed normal respiration, have been unattainable; and although many investigators have estimated normal respiration by doubling routine metabolism, such a process is felt to be too subjective by Hoss and Peters (in press).

Considering the requirement for information on fish metabolic needs under natural conditions, it appears that our method of estimating the daily rations of postlarval fishes has potential value. Our estimates of daily rations were higher or equal to those rations estimated from oxygen consumption measurements. The observed differences in rations (Table 5) are reasonable if we assume that oxygen consumption measurements, particularly those of Hoss, are closer to routine respiration than to normal. The Hoss data have the lowest values, followed by the Hettler data. These differences, although probably not significant, are reasonable because the less restrictive system provided in the flowing water respirometer allowed the fish to move about in a manner similar to that in natural water. The lack of feeding activity by fish during respiration mea-

surements and the respective decrease in oxygen consumption (Warren and Davis 1967) also should account for a lesser daily ration.

Based on earlier metabolic measurements, Thayer et al. (1974) estimated a daily ration of 1.04 cal/fish per day for larval fishes in the Newport River estuary during January and February. They indicated that, with larval energy requirements of this magnitude and a 90% assimilation efficiency, the larvae would be required to graze on an average of 10% of the zooplankton population per day. Furthermore, they suggested that this need may indeed have accounted for decreases in zooplankton observed in the estuary during spring. Our daily rations, based on feeding periodicity and evacuation (Table 5), are somewhat larger and tend to support the conclusion, assuming larval densities similar to those presented by Thayer et al. that larval fishes may have a significant impact on copepod populations in this system.

ACKNOWLEDGMENTS

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